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Meta-analysis of the relationship between salinity and molluscs in tidal river estuaries of southwest Florida, U.S.A.

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Abstract: The estuaries and rivers of the western coast of Florida have been under intense study for some time to identify relationships between inflows, salinity, and natural resources. The molluscs have been shown to be especially sensitive to salinity in other parts of the world. The current study performed a meta-analysis of existing data sets of southwest Florida mollusc communities to identify salinity-mollusc relationships at regional scales. The mollusc species are controlled more by water rather than the sediment they live in or on. The most important variable correlated with mollusc communities was salinity, which is a proxy for freshwater inflow. Although total mollusc abundance was not a good indicator of inflow effects, certain indicator species characterized salinity zones in southwest Florida rivers. *Corbicula fluminea* (Müller, 1774), *Rangia cuneata* (Sowerby, 1831), and *Neritina usnea* (Roding, 1798) were the only common species that occurred in the oligohaline zone at salinities below 1 psu. Although *C. fluminea* was the best indicator of freshwater habitat, it is a non-native, invasive bivalve species. The bivalve *R. cuneata* is an indicator of mesohaline salinity zones with an estimated tolerance of up to 20 psu. The gastropod *N. usnea* is also common in fresh to brackish-water salinities. *Polymesoda caroliniana* (Bosc, 1801) was present at salinities between 1 and 20 psu, which span the oligohaline and mesohaline zones. *Tagelus plebeius* (Lightfoot, 1786), *Crassostrea virginica* (Gmelin, 1791), *Mulinia lateralis* (Say, 1822), *Littoraria irrorata* (Say, 1822), and *Ischadium recurvum* (Rafinesque, 1820) are also good indicators for polyhaline salinity zones. These salinity ranges can be used to predict changes in mollusc assemblages in response to alterations in salinity that result from actual or simulated changes in freshwater inflow.

Key words: Mollusca, benthos, freshwater inflow, indicator species, water management

Estuaries are among the most productive environments on Earth (Odum 1959). The mixing of freshwater with seawater is the defining characteristic of an estuary, and thus, there is much interest in how alterations of freshwater inflow patterns might affect estuarine productivity (Montagna *et al.* 2002b). Certainly, the increasing size of the human footprint has had a dramatic effect on altering the courses and characteristics of rivers, streams, and lakes; these watershed-level changes have had effects on downstream estuaries in the west (Kimmerer 2002) and Gulf of Mexico coasts (Alber 2002, Powell *et al.* 2002) of the U.S.A. To identify the effects of altered flow, ecological indicators must be developed. Molluscs are ideal organisms to indicate inflow effects because of their life habits and feeding modes (Estevez 2002). Molluscs have well-defined relationships between species distributions and physicochemical variables that are affected by freshwater inflows, *e.g.* salinity (Montagna and Kalke 1995). Filter or suspension-feeding molluscs also depend on primary productivity in the water column for food, which is also affected by nutrients carried by freshwater inflow into estuaries.

The Mote Marine Laboratory (MML) and the Southwest Florida Water Management District have completed studies of mollusc distributions for six tidal rivers in southwest Florida located between the Springs Coast, Charlotte Harbor, and Tampa Bay (Fig. 1). A consistent methodology was used in these studies for the Peace River, Alafia River, Myakka River, Weeki Wachee River, Shell Creek, and the Shakett Creek Dona/Roberts Bay system (MML 2002, 2003, Estevez 2004a, 2004b, 2005). Extensive environmental data also exists for freshwater inflows and physicochemical variables (*e.g.*, salinity, dissolved oxygen, pH, and sediment characteristics) in these systems that cover the period of mollusc data collection. Although there have been studies of individual river and creek systems in Florida, there has not been an effort to combine data from many tidal rivers to quantify factors that affect mollusc distributions at the regional scale. Understanding the relationships between salinity and other environmental parameters that relate to mollusc distributions is important to evaluate the freshwater flow requirements needed to protect the natural resources in coastal ecosystems.

The overall goal of the current study was to (1) identify indicator species of freshwater inflow effects and (2) to better define the physical and chemical requirements of mollusc species that inhabit tidal river systems in southwest Florida.

The purpose was to synthesize existing information on the relationships between freshwater inflows and the distribution of mollusc populations among the tidal rivers of southwest Florida. The approach used in this project was to organize the mollusc and environmental data from the six tidal river systems into one database with a common format, to find the appropriate spatial scales in the data so that the different tidal rivers could be compared, and to perform a multivariate analysis on the combined data sets.

MATERIALS AND METHODS

Study area

The study sites were all located on the west coast of peninsular Florida (Fig. 1). They group into four areas of the coast: Weeki Wachee River estuary, Alafia River in Tampa Bay, Curry Creek and Shakett Creek located in the Dona/Roberts Bay estuary, and Charlotte Harbor estuary.

Charlotte Harbor bay and estuary complex contained six of the 10 sites studied, and four of the six were in the arm of Charlotte Harbor that is dominated by the Myakka River. There were three sites that were connected to the Myakka River: (1) Big Slough is near the 14 km marker, (2) Deer Prairie Creek is near the 19 km marker, and (3) Blackburn Canal is near the 32 km marker. The eastern arm of Charlotte Harbor is dominated by the Peace River, which is connected to Shell Creek near the 15 km marker. The Peace River ecosystem has been sampled three times: twice in the Peace River itself and once just in Shell Creek.

Shakett and Curry Creeks are located in the Dona/Roberts Bay complex in the region designated as the Venice Estuary. This area is north of, but adjacent to, the Charlotte Harbor estuary. Shakett Creek ends in Dona Bay and Curry Creek ends in Roberts Bay.

The Alafia River is about 80 km long and drains into Tampa Bay. Further north are the two small tidal rivers: the Weeki Wachee and the Mud Rivers. The Weeki Wachee River is a small, spring-fed system in which the penetration of brackish water is generally less than 2.5 km upstream from the river mouth. Mud River, which is also spring-fed, joins the Weeki Wachee about 1.4 km upstream of the river mouth. While the upstream reaches of the Weeki Wachee are fresh, the Mud River receives flow from brackish springs and salinity in the Mud River increases upstream toward the river head.

Mollusc data

Data for a meta-analysis on molluscs were extracted from several reports designed and implemented by the Mote Marine Laboratory (MML) (MML 2002, 2003, Estevez 2004a, 2004b, 2005). The data sets were complex and had to

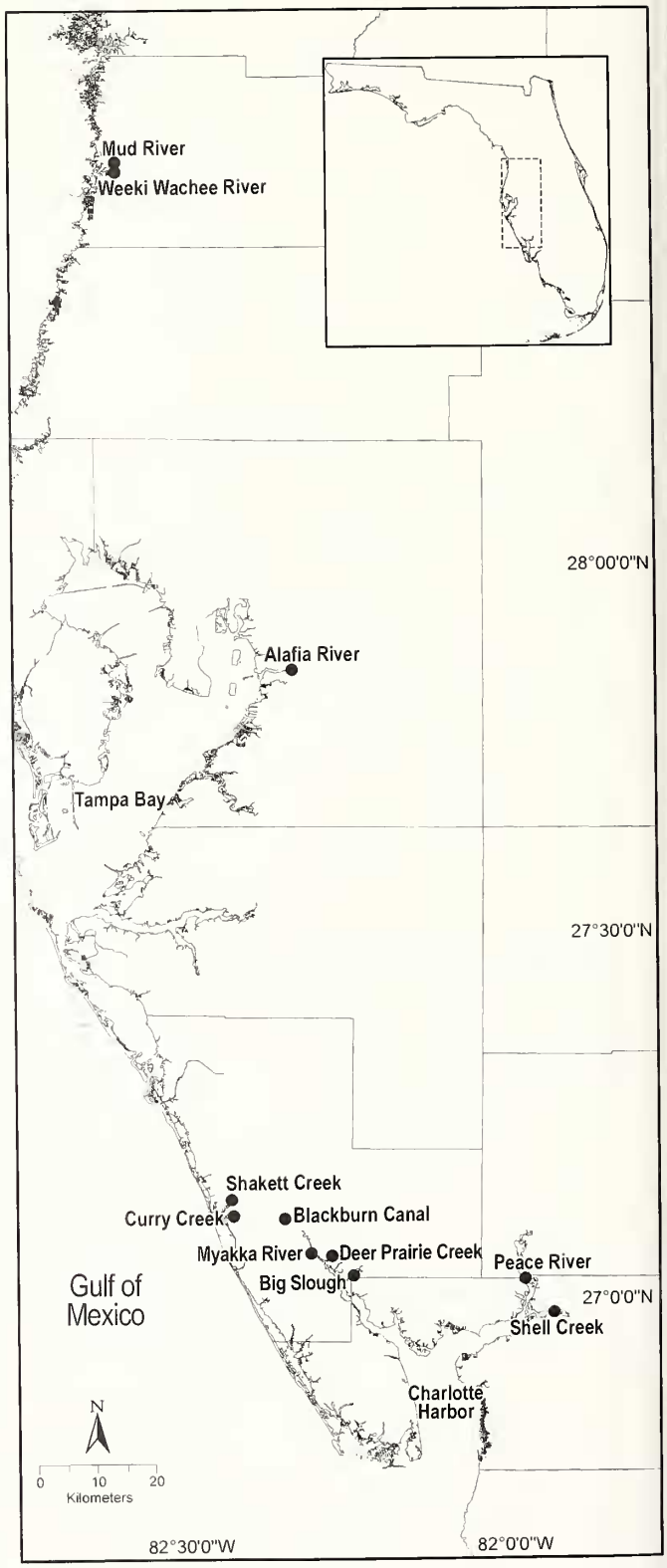

Figure 1. Map of the west coast of Florida showing the study sites.

be concatenated, merged, and formatted prior to analysis. The initial steps in database creation were to determine the relationship between site designations in the data set, if there were any differences in the actual sampling designs in the different rivers, and if there were aggregation relationships among the rivers (Table 1).

The sampling design employed by MML consists of molluscs being sampled along transects within each river system. The transects run lengthwise originating at the mouth of each river, heading upstream; hence, distance and station number names increase with freshwater influence. The original data sets varied uniquely among river systems; however, all samples were characterized by distance along the river transect and the mollusc species composition. These distances represented the stations within the river site, and a total of 180 such stations were sampled across all sites (Appendix 1). At each sampling location, molluscs were sampled systematically across the river channel perpendicular to the river centerline so that samples were collected from all major habitats found in mid-channel, shallow subtidal, and intertidal areas. Most sampling locations were spaced at half-kilometer intervals.

For each sampling event, the variables reported included the number of juvenile molluscs, the number of live molluscs, the number of dead molluscs, the size of shells, and whether the samples were taken from the subtidal or intertidal area of the river system. For all statistical analyses in the current study, mollusc counts from the subtidal and intertidal zones of each station were combined. Sample area was 0.464 m^2, and the raw counts were converted to abundance of individuals per square meter (n m^{-2}) for all univariate and multivariate analyses. For the current study, meta-analysis was focused on live molluscs; however, the dead shells do provide information on historical communities.

Samples from multiple years of sampling were found only from the Peace River (Table 1). For the purpose of the current study, the sampling stations at Peace River were averaged over the two years they were sampled (1999 and 2000). Combining the two years of data was supported in part by the absence of evidence for shell drift.

To enable a meta-analysis that simultaneously compares all rivers using multivariate methods, the distance along each transect had to be standardized. To do this, the distance from each river's mouth of each sampling station was aggregated into 2-km segment bins (Appendix 1). This was performed by rounding the actual distance from the mouth of the river (in kilometers) to increments of two. Each segment was numbered as the midpoint of the actual distance, thus a segment labeled 2 km would encompass stations found at 1.0 km to 2.9 km of a transect. Overall, 67 new stations, or 2-km segments, were created for analysis. Because more than one sampling station occurred within many new 2-km segments, species abundances were averaged across stations within each new 2-km segment prior to analysis to ensure a balanced sampling design.

The scientific names of all the species were verified and made consistent across all data sets. In addition, the full taxonomic description was verified. The convention for species names and taxonomy used in the current study is based on the Species 2000 and Integrated Taxonomic Information System (ITIS) Catalogue of Life: 2006 Annual Checklist (Bisby *et al.* 2006, http://www.sp2000.org).

Hill's number one (N1) diversity index was used to report species diversity (Hill 1973). Hill's N1 is the exponential form ($e^{H'}$) of the Shannon-Weaver diversity index H′. N1 was used because it has units of numbers of dominant species, and it is easier to interpret than most other diversity indices (Ludwig and Reynolds 1988).

Multivariate analyses

Community structure of mollusc species was analyzed by non-metric multi-dimensional scaling (MDS). All multi-

Table 1. Location of sites within river systems, sampling year(s), and time period that water hydrography data were collected.

Estuary	River system	Site (or creek)	Molluscs	Hydrography
Tampa Bay	Alafia	Alafia	2001	Jan 1999-Dec 2003
Charlotte Harbor	Myakka	Big Slough	2004	—
Charlotte Harbor	Myakka	Blackburn	2004	—
Charlotte Harbor	Myakka	Deer Prairie	2004	—
Charlotte Harbor	Myakka	Myakka	2004	Feb 1998-Mar 2005
Charlotte Harbor	Peace	Peace	1999 & 2000	Aug 1996-Dec 2004
Charlotte Harbor	Peace	Shell	2004	Feb 1991-Dec 2004
Venice	Dona/Roberts Bay	Curry	2004	Aug 2003-May 2005
Venice	Dona/Roberts Bay	Shakett	2004	Aug 2003-May 2005
Weeki Wachee	Weeki Wachee	Mud River	2005	July 2003-May 2005
Weeki Wachee	Weeki Wachee	Weeki Wachee	2005	July 2003-May 2005

variate statistical analyses were performed using Primer software (Clarke and Warwick 2001). The MDS procedure was used to compare mean abundances of individuals of each species for each river-site-segment combination. The MDS analysis was completed using a Bray-Curtis similarity matrix on log-transformed ln (x + 1) data. The distance between river-site-segment combinations in the MDS plot can be related to community similarities or differences between rivers, sites, and segments. Differences and similarities among communities were highlighted based on cluster analysis calculated from the similarity matrix. A subset of species that represented the spatial pattern in an MDS plot was determined using the BVSTEP procedure. The BVSTEP procedure employs a step-wise approach to determine the minimum subset of species that can yield the same pattern of community structure obtained from the entire data set (Clarke and Warwick 1998).

Physicochemical variables

Physicochemical data for each tidal river system included profiles of temperature, dissolved oxygen, salinity, and pH taken along all transects. Profiles were measured at various distances along the transects in each river on multiple dates over a period of 2-13 years. The length of period and actual years sampled varied for each river (Table 1). As with the mollusc data, the distance along each transect was converted into the same 2-km segments for the physical data. The four water hydrography parameters measured (temperature, dissolved oxygen, salinity, and pH) were all averaged by transect segment and river.

Principle Components Analysis (PCA), a parametric multivariate method, was used to determine differences for the environmental measurements among river-segment combinations. As with MDS, the distance between river-segment combinations in the PCA plot can be related to actual similarities or differences in water hydrography between river-segment combinations.

Sediment

Samples along each transect were also analyzed by MML for sediment characteristics. Sediment grain size distributions (median, mean, % sand, % silt, % clay, skewness, kurtosis), sediment moisture, and the proportion of organic material present in the sediment were measured.

Relating molluscs and environmental factors

Relationships between mollusc communities and environmental factors were investigated using the Biota-Environment (BIO-ENV) procedure using Primer software (Clarke and Warwick 2001). The BIO-ENV procedure is a multivariate method that matches biotic (*i.e.*, mollusc community structure) with environmental variables. This is carried out by calculating weighted Spearman rank correlations (ρ_w) between sample ordinations of all environmental variables and biotic variables (Clarke and Ainsworth 1993). Correlations are then compared to determine the best match. The BIO-ENV procedure uses different numbers of abiotic variables in calculating correlations to investigate the different levels of environmental complexity. For this study, the mollusc species abundance MDS ordination was compared with all physicochemical and sediment variables. A total of 49 of the 67 river-segment combinations were used in the multivariate analysis because these stations had all sediment, physiochemical, and mollusc data necessary for analysis. The significance of relationships were tested using RELATE, a non-parametric form of the Mantel test. The BIO-ENV and RELATE procedures were calculated with Primer software (Clarke and Warwick 2001).

Salinity was used as a proxy for distance from a freshwater source because salinity increases as distance from the freshwater source increases. Salinity was directly compared with individual species abundances, total mollusc abundances, and mollusc diversity.

The relationship between mollusc abundance, diversity, and salinity were examined with a non-linear model, which was used successfully in Texas estuaries (Montagna *et al.* 2002a). The assumption behind the model is that there is an optimal range for salinity and values decline prior to and after meeting this maximum value. That is, the relationship resembles a bell-shaped curve. The shape of this curve can be predicted with a three-parameter, log normal model:

$$Y = a \times \exp(-0.5 \times (\ln(X / c) / b)^2)$$

The model was used to characterize the nonlinear relationship between a biological characteristic (Y, *e.g.*, abundance or diversity) and salinity (X). The three parameters characterize different attributes of the curve, where a is the peak abundance value, b is the skewness or rate of change of the response as a function of salinity, and c the location of the peak response value on the salinity axis (Montagna *et al.* 2002a). The model was fit to data using the Regression Wizard in SigmaPlot (version 10) which uses the Marquardt-Levenberg algorithm to find coefficients (parameters) of the independent variables that give the best fit between the equation and the data (Systat 2006).

RESULTS

Physical environments

With the exception of Mud River, salinity decreased with distance from the river or creek mouth in all the river systems (Fig. 2). Because rivers and transects in each river were different, the length of each transect covered different

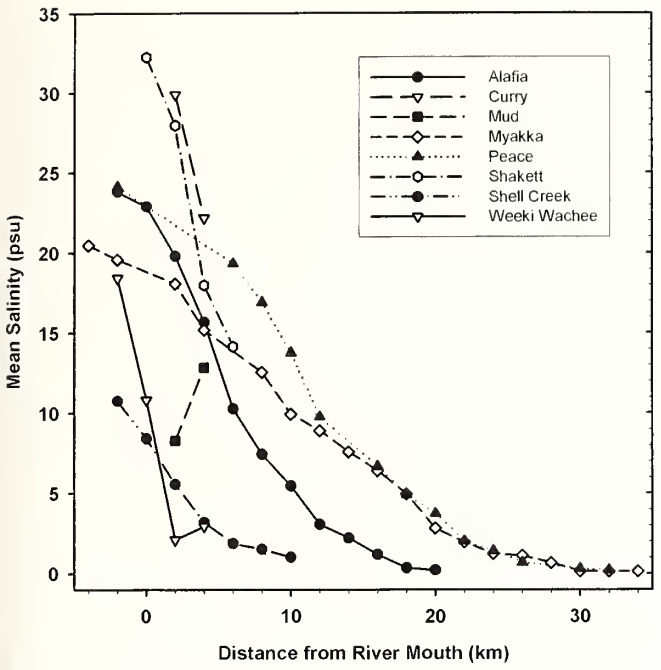

Figure 2. Mean salinity along transects at each creek /site system.

salinity ranges; thus, a km segment number in one river did not correspond to a similar salinity range in another system. The transects of the Alafia, Myakka, and Peace Rivers were at least 20 km long and had mean salinity ranges between 20 and 25 psu. Although the Shakett Creek and Weeki Wachee River transects covered less than 8 km, they also covered a mean salinity range of at least 15 psu. The transects in Curry Creek, Shakett Creek, and Mud River did not extend to freshwater, as did the transects on the other river systems. A salinity barrier on Shakett Creek truncates this river and structurally isolates a freshwater zone under most flow conditions. As described earlier, the Mud River is an unusual system that is fed by brackish springs and salinity increases toward the river head. Only two transect segments were sampled in each of Curry Creek and the Mud River.

The principal components (PC) analysis reduced the four environmental variables of salinity, temperature, pH, and dissolved oxygen (DO) into two PC axes. The first (PC1) and second (PC2) principal components of the physicochemical data explained 98.7% and 0.7% of the variation within the data set, respectively (total 99.4%; Fig. 3). PC1 was dominated by salinity and pH differences and PC2 by temperature (Fig. 3A). Dissolved oxygen differences were not important because it varied little from the origin. Thus, PC1 represents changes over distance along the transects or between rivers, and PC2 represents water body and temporal change, with higher temperatures as higher PC2 values. The PC analysis demonstrates that Alafia, Weeki Wachee, Sha-

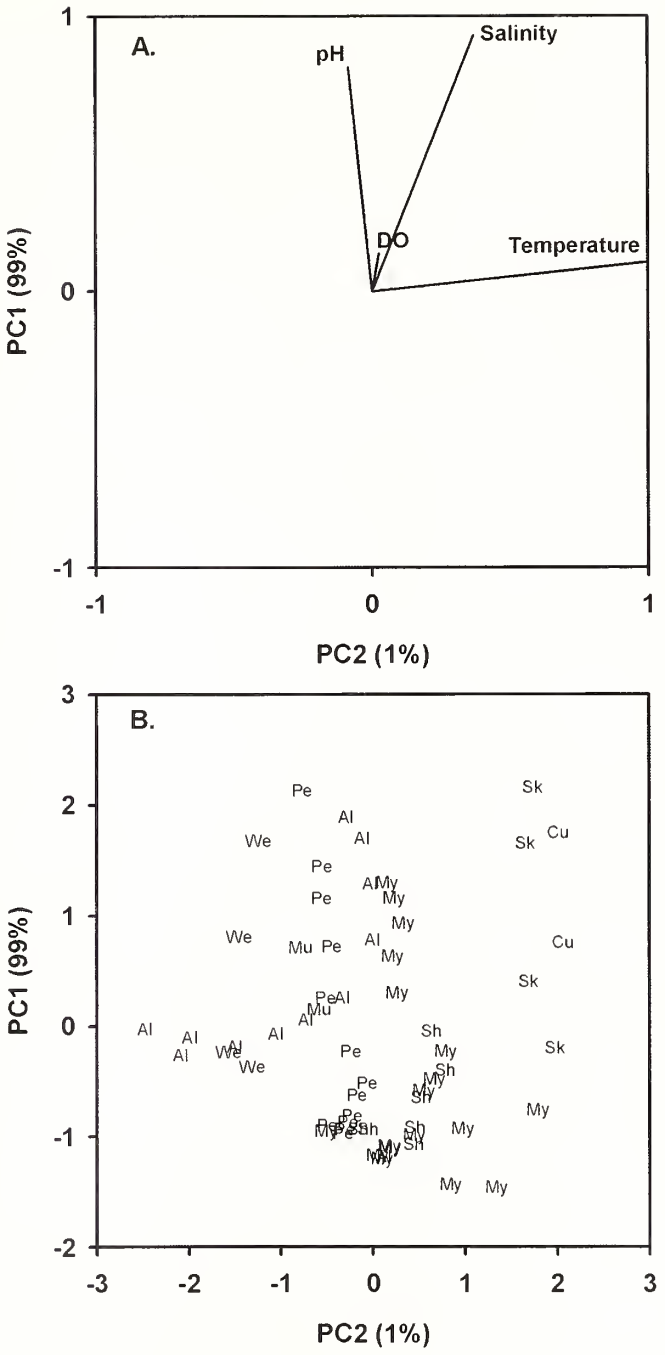

Figure 3. Principal Components Analysis (PCA) of water hydrography in southwest Florida rivers. A, Principal Component variable loadings. B, Transect segment-river station scores. Symbol key: Al, Alafia River; Cu, Curry Creek; Do, Dona/Roberts Bay; My, Myakka River; Pe, Peace River; Sk, Shakett Creek; Sh, Shell Creek; We, Weeki Wachee River.

kett, Curry, and Myakka are all distinct water bodies (Fig. 3B). The differences are primarily a result of separation along the PC2 axis. Shakett, Curry, and Myakka had similar temperature conditions but were distinct from the Alafia and Weeki Wachee in this regard. Separation along PC1 and PC2 indicates the Peace and Myakka Rivers were very similar to one another with respect to their physical characteristics. The Alafia River had a unique pattern where at low salinities temperatures increased, but at high salinities temperatures were similar.

Taphonomy

Examining the fossil shells or death-assemblages, *i.e.*, taphonomy, is a good technique to understand the derivation of extant benthic communities because it is an indicator of the living community prior to sampling and between sampling occasions (Powell *et al.* 1986). The total abundance was similar with a mean of 95 m^{-2} relict shells compared to a mean of 82 m^{-2} live shells. The proportion of dead shells to live shells was similar overall because a paired-difference test was not significantly different ($P = 0.7822$). A total of 56 relict species were found (Appendix 2). However, 22 more species were found among relict shells than live shells. This does not mean that species have gone extinct or are no longer found in the study area. Shells can be transported after death, and the age of the shells are unknown; therefore, the remainder of this current report focuses on the living fauna. However, there was no evidence from field observations that shells were transported in these low-flow rivers and creeks.

Mollusc community structure

A total of 33 live species were found in all of the rivers sampled (Appendix 2). Of these, 25 species were bivalves and eight species were gastropods. Two families of bivalves, Tellinidae and Mytilidae, were represented by four species each, and there were three species of Veneridae. Otherwise, all families were represented by only one or two species.

The dominant species was the Asian Clam *Corbicula fluminea* (Müller, 1774) an exotic species introduced to Florida waters (Appendix 3). The large number of *C. fluminea* was due to very high densities of this species in the tidal freshwater reaches of the Peace River; a lower density was found in the Myakka River, and five rivers had none. *Corbicula fluminea* was found in 27 river-segments and had a mean density of 33 individuals m^{-2} throughout all 67 river-segments. This represented 40% of total mean abundance. The next four most dominant species were *Polymesoda caroliniana* (Bosc, 1801; 11%), *Rangia cuneata* (Sowerby, 1831; 8%), *Tagelus plebeius* (Lightfoot, 1786; 6%), and *Amygdalum papyrium* (Conrad, 1846; 5%). These top five most abundant molluscs were bivalves and comprised 70% of all specimens found. The dominant gastropod *Neritina usnea* (Roding, 1798) was the sixth-ranked species in dominance (4% of total mean abundance). The second-most dominant species *P. caroliniana* was found in 35 river-segments.

Dominance patterns were different in different rivers (Appendix 3). For example, *Corbicula fluminea* was dominant only in the Peace and Myakka Rivers. In contrast, *P. caroliniana* was dominant in Shell Creek and Big Slough, and the second-most dominant species in Deer Prairie Creek, Myakka, and Weeki Wachee Rivers. *Rangia cuneata* was dominant in Deer Prairie and was the only organism found in Blackburn Canal. *Tagelus plebeius* was co-dominant in Weeki Wachee and the dominant species in Mud River and Curry Creek. *Geukensia granosissima* (Sowerby, 1914) was dominant in the Alafia River, and *Crassostrea virginica* (Gmelin, 1791) was co-dominant in Weeki Wachee and dominant in Shakett Creek. However, the distribution of *C. virginica* in the Weeki Wachee River was largely limited to individuals located near the river mouth.

Similarity in mollusc communities among the river-segment sites is generally low (Fig. 4). All of the river-segment combinations are found in associations of groups of

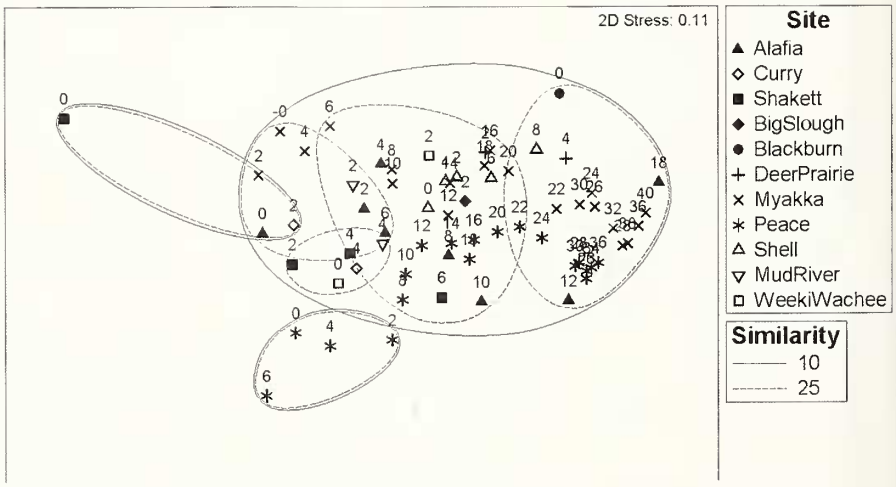

Figure 4. Relationships between mollusc communities from multi-dimensional scaling (MDS) analysis. Symbols represent the river or creek site with shape and color, and the km segment number is listed above the river symbol. Segment 16 from the Alafia River is outside the range of this plot. Similarity is indicated with lines drawn around points.

no more than 10% similarity. At the 10% similarity level there are three groups, two smaller groups with low station numbers (*i.e.*, more marine conditions) and one large group. At the 25% similarity level, the large group splits into 4 smaller groups. Although the pattern of river-segment groupings is based on 33 species, it is being driven by just seven species: *Corbicula fluminea*, *Crassostrea virginica*, *Littoraria irrorata* (Say, 1822), *Neritina usnea*, *Polymesoda caroliniana*, *Rangia cuneata*, and *Tagelus plebeius* (BVSTEP, rho > 0.95, r = 0.96). These species drive the trend in which downstream segments close to marine sources (with low 2-km segment numbers) tend to group to the left, while higher segment numbers groups to the right in the MDS plot (Fig. 4).

The four groups at the 25% level within the large central group at the 10% similarity level (Fig. 4) can be explained based on the distribution of three species. From left to right in Fig. 4, the station groups are dominated by *Crassostrea virginica*, *Polymesoda caroliniana*, and *Corbicula fluminea*. Two groups fell outside the 10% similarity level. One group had four Peace River segments (0, 2, 4, and 6). The other group had just one Shakett Creek 0 segment, and this was most different from all other segments because it had only two rare species: *Chione cancellata* (Linnaeus, 1767) and *Cyclinella tenuis* (Recluz, 1852). The 16-km segment of the transect in the Alafia River was so different from all others that it is not included in the MDS plot. This station is 100% different from all of the other stations sampled, because the station had only one mollusc present, an unidentified snail of the family Planorbidae, which was not found in any of the other river systems.

Mollusc-environment relationships

Two approaches are used to relate molluscs to the environment, but in all cases salinity is used as the surrogate for inflow. One approach is to relate (by univariate or multivariate models) salinity with abundance, diversity, or community structure. The second approach is to examine the relationship between abundance and salinity to identify those species or species groups that might have optimal salinity ranges.

For the first approach, a non-parametric multivariate analysis procedure (BIO-ENV) was used to identify the combinations of environmental variables that could best predict mollusc abundance. Out of 62 transect-segments sampled for water hydrography and 67 transect-segments sampled for molluscs, there were only 45 common transect-segments that could be analyzed using BIO-ENV because of missing water hydrography data in the other transect-segments. Salinity, temperature, and pH were the environmental variables that correlated the highest with the mollusc community distributions ($\rho_w = 0.612$). The RELATE procedure indicated that this correlation was significant ($P < 0.001$). The single physical variable that correlated the highest with mollusc communities was salinity ($\rho_w = 0.566$). In fact, salinity was the only variable that fit the community distributions in all the tests. The water hydrography variables had higher correlations with the mollusc communities than any single, or combination of, sediment characteristics. Of the sediment variables, median and mean grain size fit best, but all sediment variables were selected after salinity, temperature, and pH. This indicates that overlying water properties, especially salinity values, have more control on the mollusc communities than the sediment characteristics.

In the second approach, total mollusc abundance did not correlate with salinity among all rivers. The highest abundances occurred at low salinities, but this is attributed to the large population of *Corbicula fluminea* that occurred in the Peace River at low salinities. Mollusc diversity increased with salinity, particularly as salinity increased from 0 to 2 psu, but the correlation was weak. Hill's N1 values were consistently close to one where mean salinity was close to one; however, as salinity and overall N1 increased, so too did the range of N1 values.

Two rivers, the Myakka and Peace, were sampled across long transects (Fig. 2). Examining distributions along salinity gradients in these two rivers separately avoids bias due to differences between the systems. In both rivers there were strong relationships between both diversity and abundance with salinity where abundance and diversity increased with increasing salinity, then peaked, before declining (Fig. 5). This response emulates a 3-parameter log-normal distribution, which was found to fit total macrofauna abundance in a Texas estuary (Montagna *et al.* 2002a). The nonlinear relationship between salinity and diversity was stronger in the Peace River than the Myakka River, based on the probability levels (P) and goodness of fit parameters (R^2) (Table 2).

The ten dominant species were examined for correlations with salinity (Table 3). *Corbicula fluminea* was found only where mean salinities were <7 psu, but it was most common where mean salinities were ≤2 psu (Fig. 6A). However, the maximum salinity value (parameter c in Table 2) was 0.6 psu. *Corbicula fluminea* occurred at abundances higher than 10 m^{-2} only in the Myakka and Peace Rivers. *Polymesoda caroliniana* was found in all river systems and occurred where salinities ranges from 1 to 20 psu (Fig. 6B) while peaking at 5 psu (Table 2). Both *P. caroliniana* and *C. fluminea* are in the same family (Corbiculidae). *Rangia cuneata* and *Tagelus plebeius* were found in low to moderate salinities and occurred at salinity peaks of 4 and 7 psu respectively (Figs. 6C-D). *Crassostrea virginica* and *Geukensia granosissima* were generally found at higher salinities, as indicated by salinity peaks of 24 and 10 psu, respectively. *Mulinia lateralis* ranged from 5 to 15 psu, and the model cal-

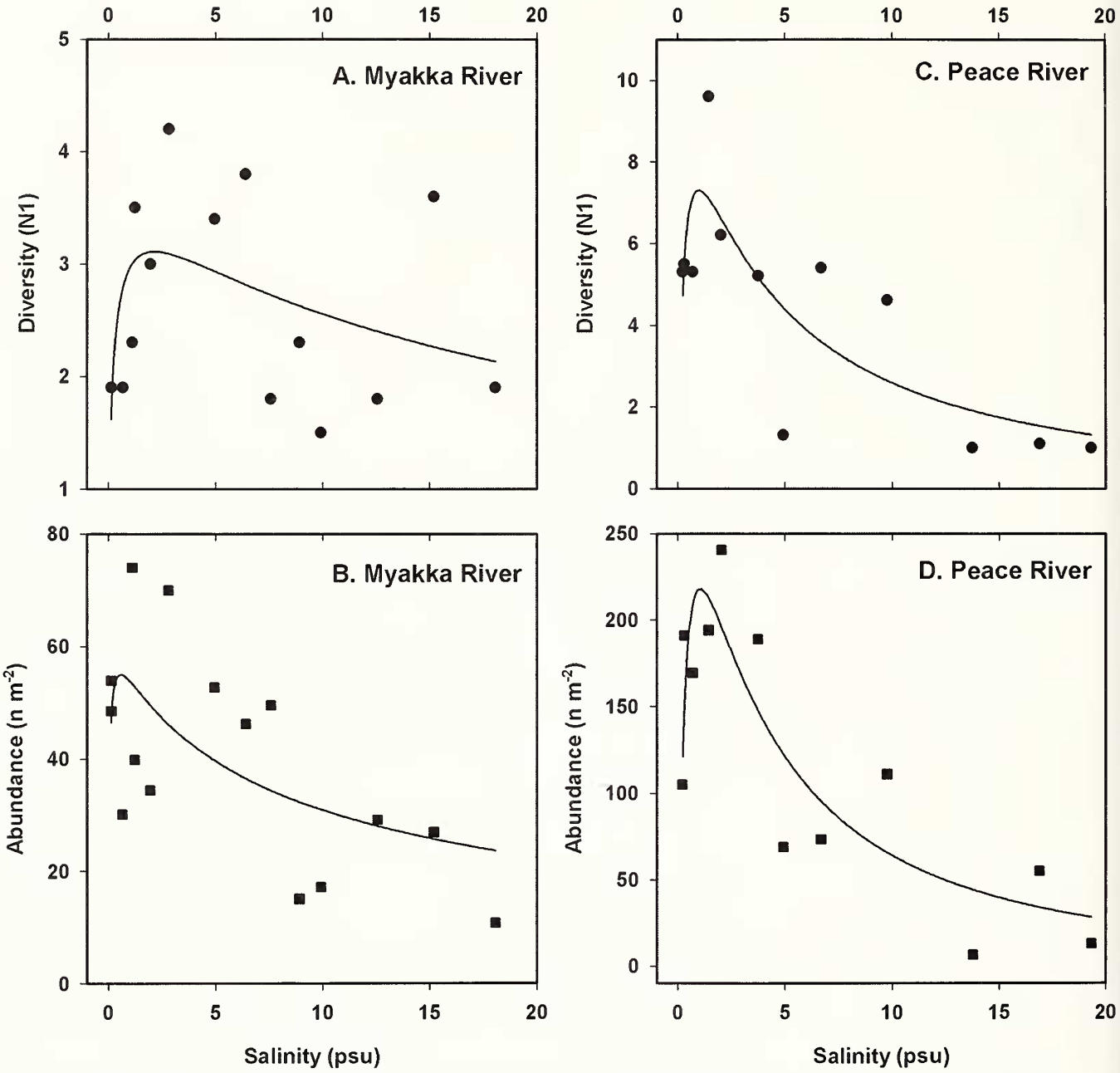

Figure 5. Relationship between total mollusc diversity (A) and abundance (B) vs. salinity at Myakka River and diversity (C) and abundance (D) versus salinity at Peace River. Circles, Hill's N1 diversity index; squares, abundance.

culated a peak at 14 psu. According to the model, *Neritina usnea* abundance did not change with salinity ($P = 0.43$). *Littoraria irrorata* and *Ischadium recurvum* were found over a wide range of salinities, with peak salinities at 14 and 12 psu, respectively. Two other species, *Amygdalum papyrium* and *Tellina versicolor*, occurred in less than 9 segments, precluding an estimation of the salinity range.

DISCUSSION

The overall purpose of this project was to better define the biogeography, community structure, and the physical and chemical requirements of mollusc species that inhabit tidal river systems in southwest Florida. To meet this purpose, an inter-river meta-analysis was performed to examine

Table 2. Parameters from nonlinear regressions to predict mollusc characteristics from salinity. These parameters are represented on lines in Figs. 5 and 6. Probability (P) that model fits the data, percent of variance explained by data (R^2), parameters for maximum biological value (a), rate of change (b), and salinity in which maximum abundance occurs (c), and standard deviation for parameters in parentheses. N1, Hill's diversity index; n, abundance (individuals per m^2); all species are n m^{-2}.

Variable	P	R^2	a	b	c
Myakka N1	0.1658	0.26	3.11 (0.36)	2.45 (0.65)	2.15 (0.86)
Myakka n	0.0682	0.36	54.9 (7.9)	2.63 (0.84)	0.59 (0.41)
Peace N1	0.0098	0.64	7.29 (1.02)	1.61 (0.31)	0.99 (0.28)
Peace n	0.0013	0.77	218 (24.8)	1.44 (0.20)	1.05 (0.20)
Neritina usnea	0.4320	0.03	4.92 (1.71)	2.96 (2.77)	0.45 (1.33)
Corbicula fluminea	0.0001	0.31	178 (43.2)	0.78 (0.19)	0.63 (0.18)
Rangia Cuneata	0.0001	0.38	27.3 (4.8)	0.49 (0.08)	3.69 (0.31)
Polymesoda caroliniana	0.0001	0.32	28.8 (5.1)	0.66 (0.13)	4.89 (0.63)
Tagelus plebeius	0.0003	0.28	15.4 (3.0)	0.48 (0.12)	7.30 (0.90)
Geukensia granosissima	0.0001	0.77	156 (11.9)	0.006 (3e-7)	10.3 (3e-6)
Ischadium recurvum	0.0169	0.16	5.68 (1.81)	0.31 (0.11)	12.3 (1.3)
Mulinia lateralis	0.0001	0.37	324 (53.3)	0.006 (3e-7)	13.6 (8e-6)
Littoraria irrorata	0.0001	0.33	6.43 (1.28)	0.31 (0.07)	13.8 (0.98)
Crassostrea virginica	0.0001	0.33	19.3 (4.2)	0.18 (0.04)	22.4 (1.0)

Table 3. Salinity range of twelve most abundant species.

Species	Salinity range (psu)	Transect segments with species present
Corbicula fluminea	<7 (most ≤2)	20
Polymesoda caroliniana	1 to 20	32
Rangia cuneata	<16 (most ≤10)	23
Tagelus plebeius	>2	25
Geukensia granosissima	10 to 24	5
Amygdalum papyrium	2 to 20	8 (7 in Peace R.)
Crassostrea virginica	>7	13
Mulinia lateralis	>2	10
Neritinia usnea	<18	20
Tellina versicolor	2 to 18	7 (all in Peace R.)
Littoraria irrorata	>2	17
Ischadium recurvum	>6	11

relationships between the distribution of mollusc populations both within and among tidal river estuaries and tidal river locations. The meta-analysis combines independent studies to reach general conclusions (Gurevitch and Hedges 2001). The sampling gear and spatial sampling strategies were consistent for both water hydrography and mollusc data, making this meta-analysis a simple task. Although these data were collected without specific regard to a regional scale design and analysis, the data fit well into a sampling design, even though all samples were not taken in the same year (Table 1). Two exceptions to this lack of synoptic sampling were the Myakka and Dona/Roberts Bay systems. However, all the rivers exhibited distinct changes in their water hydrography characteristics and mollusc community composition along the estuarine gradient. Therefore, analysis of these data provides meaningful information on how environmental factors affect the distribution and abundance of mollusc populations within these tidal river ecosystems.

River systems were strikingly different. The mollusc communities among all the river stations shared <25% species in common. Although sampling occurred over different years, there were community similarities at similar transect segments among rivers. There were upstream clusters, downstream clusters, and larger clusters of intermediate range transects. The segments with the most similar mollusc communities occurred in the most upstream segments of the Peace, Myakka, and Alafia Rivers. These segments had the most stable, and lowest mean salinities with minimal tidal influence. Further downstream, freshwater influence decreased and salinity was more variable, which allowed different species and communities to persist, compared to stable upstream waters. Other factors such as tides, waves, currents, and inshore geomorphology create diverse habitats both within and between estuarine river systems. This increase in physical diversity from upstream to downstream can cause the considerable differences found in mollusc communities along the salinity gradient and among the rivers. The heterogeneity of the salinity regimes is why the river systems share <25% of species in common.

The highest correlations between physical variables and mollusc communities were with salinity. Salinity differences were, thus, more important than sediment differences in regulating mollusc communities in tidal rivers of southwest Florida. The physical variables with the highest correlations

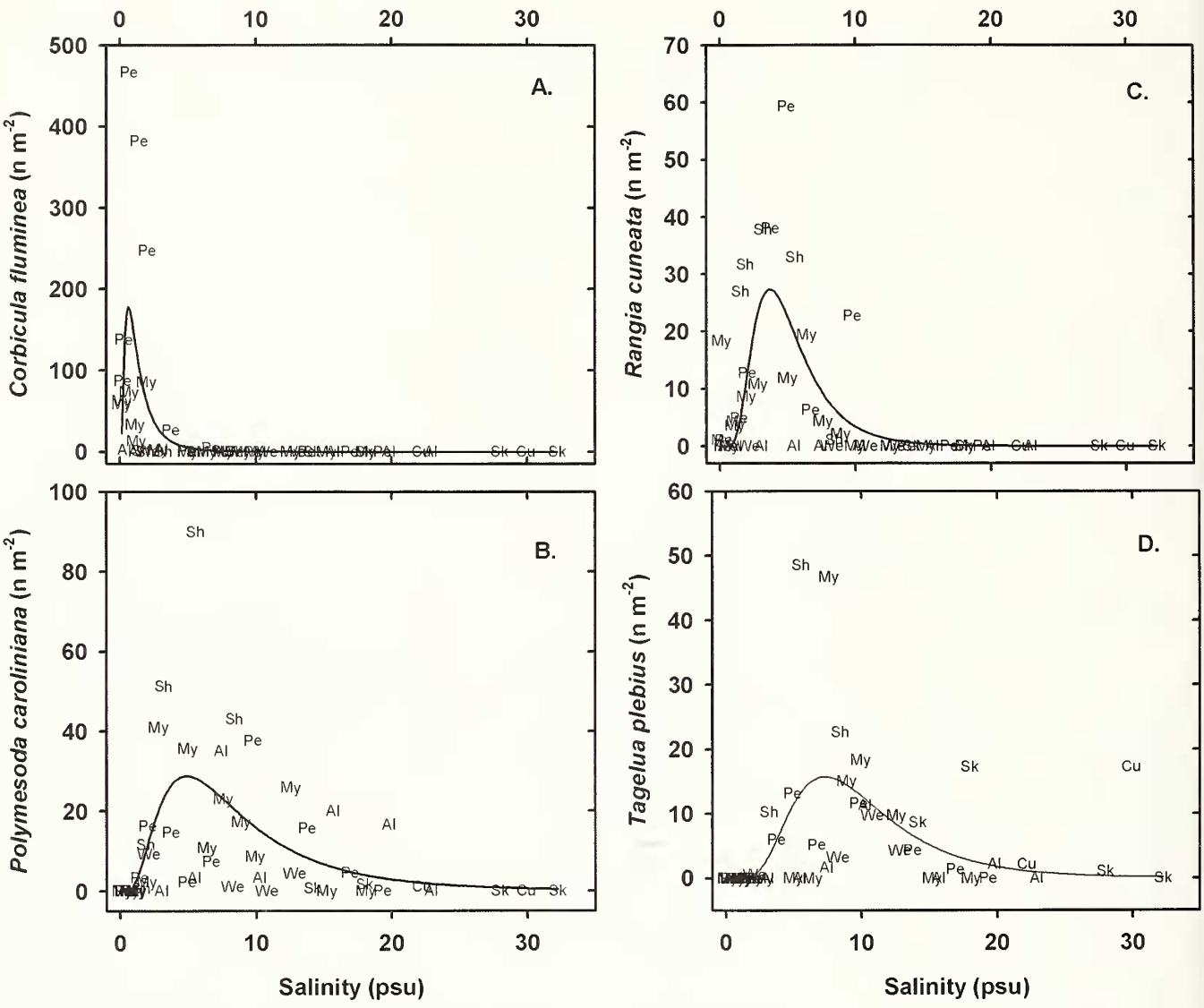

Figure 6. Relationship between salinity and species abundance. A, *Corbicula fluminea*; B, *Polymesoda caroliniana*; C, *Rangia cuneata*; and D, *Tagelus plebeius*. Symbol key: Al, Alafia River; Cu, Curry Creek; Do, Dona/Roberts Bay; My, Myakka River; Pe, Peace River; Sk, Shakett Creek; Sh, Shell Creek; We, Weeki Wachee River.

with the macrofaunal community structure almost always included salinity, temperature and pH. The best single physical indicator of mollusc communities was salinity. Thus, freshwater inflow, which is one factor controlling salinity, is an important factor influencing mollusc community structure and abundance patterns. *Corbicula fluminea*, *Rangia cuneata*, and *Neritina usnea* were the only species common to rivers, creeks, and canals that occurred at salinities below 1 psu. However, *C. fluminea* was the best indicator of freshwater habitat and is an introduced bivalve that can survive salinities up to 13 psu (Morton and Tong 1985) but usually occurs primarily in freshwater (Batelle 2000). *Rangia cuneata* is an indicator of a fresh to brackish-water (Swingle and Bland 1974, Montagna and Kalke 1995). *Neritina usnea* is also common in fresh to brackish-water salinities (Andrews 1992). *Polymesoda caroliniana* is a native, brackish-water bivalve (Gainey and Greenberg 1977) also from the family Corbiculidae. In the current study, *P. caroliniana* was present at salinities between 1 and 20 psu and was present in all creeks/sites.

Tagelus plebeius, Crassostrea virginica, Mulinia lateralis, Littoraria irrorata, and *Ischadium recurvum* are also good indicators for brackish to seawater salinities. The relationship between *C. virginica* and salinity is well known (Turner

2006). *Mulinia lateralis* prefers organically-rich muddy sediments (Grassle *et al.* 1992) and has the ability to survive short periods of anoxia (Shumway *et al.* 1993). *Mulinia lateralis* is typically found in euryhaline habitats (Williams 1984). Although these bivalves are most often found in these brackish to euryhaline salinity zones, they may also be most susceptible to predation in the same area. For example, the oyster drill *Stramonita haemastoma* (Gray, 1839) can severely crop *I. recurvum* and *Rangia cuneata* at high salinities and limit these prey to lower salinity areas along the Gulf of Mexico coast (Brown and Richardson 1988).

Total mollusc abundance and aggregated mollusc species diversity did not indicate freshwater inflow across all rivers, but were useful within rivers. In addition, the trend of transect numbers increasing from left to right in the MDS analysis is evidence of seriation (*i.e.*, linearity or spatial associations) in the mollusc communities.

In summary, from this meta-analysis of southwest Florida communities, mollusc species appear controlled more by water column hydrography rather than the sediment composition. Salinity is the most important environmental variable and is an indicator or proxy for freshwater inflow. One typical approach to link community responses inflow changes is to perform long-term studies of inflow events. The current study used spatial variability at a regional scale to capture a large range of salinity differences, and hence inflow influences. Certain indicator species have been identified that characterize salinity ranges in southwest Florida rivers. These salinity ranges may be useful in predicting mollusc community reactions to changes in freshwater inflow.

Although meta-analysis is an emerging and accepted practice, synoptic sampling over time would greatly improve the ability to accurately determine the relationships between inflow and the mollusc communities, relative to those in other regions. Synchronization of sampling and sample replication would also improve the ability to accurately correlate mollusc communities' response to freshwater inflows using the types of data analysis reported here. Nevertheless, the use of transect-segments in the current meta-analysis and comparing data from the different surveys has led to robust conclusions.

The present study clearly demonstrates that estuarine mollusc species are arrayed along horizontal salinity gradients within tidal river estuaries, with certain species being most common in low salinity zones (*e.g.*, <10-15 psu). In addition to salinity, other factors such as current velocities or the availability of detrital or planktonic food resources could contribute to mollusc distribution patterns in tidal rivers. Low salinity zones are among the habitats that are most vulnerable to impacts and loss within Gulf Coast estuaries because of proximity to human activities in adjacent uplands and the sources of pollution from the contributing watersheds (Lewis and Robison 1995, Beck *et al.* 2005). Low salinity zones are also particularly sensitive to shifts and changes in salinity regimes that could be caused by freshwater withdrawals or salinity intrusions. Given that distinct mollusc communities occur within low salinity waters, the proper management of freshwater inflows and other related watershed activities are very important for maintaining the biological integrity of mollusc populations in tidal river estuaries.

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Appendix 1. Aggregation of Mote Marine Laboratory (MML) sampling data for the current analyses. For each river-site, the new 2-km bin name created and the number of MML stations that were located within the 2-km bin.

River	Site	2-km bin name	Number of stations
Alafia	Alafia	0	2
Alafia	Alafia	2	3
Alafia	Alafia	4	4
Alafia	Alafia	6	4
Alafia	Alafia	8	4
Alafia	Alafia	10	4
Alafia	Alafia	12	3
Alafia	Alafia	16	1
Alafia	Alafia	18	1
Dona/Roberts	Curry	2	3
Dona/Roberts	Curry	4	2
Dona/Roberts	Shakett	0	1
Dona/Roberts	Shakett	2	4
Dona/Roberts	Shakett	4	4
Dona/Roberts	Shakett	6	3
Myakka	Big Slough	2	2
Myakka	Blackburn	0	1
Myakka	Deer Prairie	2	2
Myakka	Deer Prairie	4	1
Myakka	Myakka	−0	2
Myakka	Myakka	2	2
Myakka	Myakka	4	2
Myakka	Myakka	6	2
Myakka	Myakka	8	2
Myakka	Myakka	10	2

Appendix 1. (continued)

River	Site	2-km bin name	Number of stations
Myakka	Myakka	12	2
Myakka	Myakka	14	3
Myakka	Myakka	16	1
Myakka	Myakka	18	2
Myakka	Myakka	20	3
Myakka	Myakka	22	2
Myakka	Myakka	24	1
Myakka	Myakka	26	3
Myakka	Myakka	28	2
Myakka	Myakka	30	2
Myakka	Myakka	32	2
Myakka	Myakka	36	2
Myakka	Myakka	38	3
Myakka	Myakka	40	1
Peace	Peace	0	1
Peace	Peace	2	1
Peace	Peace	4	1
Peace	Peace	6	1
Peace	Peace	8	4
Peace	Peace	10	4
Peace	Peace	12	4
Peace	Peace	14	4
Peace	Peace	16	5
Peace	Peace	18	5
Peace	Peace	20	4
Peace	Peace	22	5
Peace	Peace	24	4
Peace	Peace	26	5
Peace	Peace	28	4
Peace	Peace	30	4
Peace	Peace	32	4
Peace	Peace	34	3
Peace	Peace	36	1
Shell	Shell	0	2
Shell	Shell	2	4
Shell	Shell	4	4
Shell	Shell	6	3
Shell	Shell	8	4
Weeki Wachee	Mud River	2	2
Weeki Wachee	Mud River	4	1
Weeki Wachee	Weeki Wachee	0	2
Weeki Wachee	Weeki Wachee	2	4
Total number of segment bins and stations		67	180

Appendix 2. Taxonomic list of all live and relict species found. Abundance of all relict and live individuals found per m^2 averaged over all samples (*i.e.*, river-site-segment combinations). Abbreviations: CL, Class; OR, Order; and FA, Family.

CL OR FA Species	Dead	Live
Gastropoda		
Pulmonata		
Ellobium		
Melampus sp.	0.055	0
Basommatophora		
Planorbidae		
Planorbidae (unidentified)	0.208	0.032
Neotaenioglossa		
Littorinidae		
Littoraria irrorata (Say, 1822)	0.469	1.811
Epitoniidae		
Epitonium rupicola (Kurtz, 1860)	0.031	0
Calyptraeidae		
Crepidula fornicata (Linnaeus, 1758)	0.318	0
Naticidae		
Polinices duplicatus (Say, 1822)	0.133	0.048
Cerithiidae		
Cerithium atratum (Born, 1778)	0.495	0
Triphoridae		
Triphora melanura (Adams, 1850)	0.031	0
Cephalaspidea		
Bullidae		
Bulla striata (Bruguiere, 1792)	0.073	0
Haminoeidae		
Haminoea succinea (Conrad, 1846)	0.851	1.062
Neogastropoda		
Conidae		
Conus sp.	0.010	0
Nassariidae		
Nassarius vibex (Say, 1822)	2.944	1.395
Melongenidae		
Melongena corona (Gmelin, 1791)	0.247	0.153
Muricidae		
Eupleura sp.	0.021	0
Urosalpinx tampaensis (Conrad, 1846)	0.042	0
Neritopsina		
Neritidae		
Neritina usnea (Roding, 1798)	5.990	3.028
Bivalvia		
Myoida		
Pholadidae		
Cyrtopleura sp.	0	0.008
Veneroida		
Cardiidae		
Laevicardium mortoni (Conrad, 1830)	0.497	0.131
Corbiculidae		
Corbicula fluminea (Müller, 1774)	23.306	33.107
Polymesoda caroliniana (Bosc, 1801)	13.281	9.052

Appendix 2. (continued)

CL OR FA Species	Dead	Live
Dreissenidae		
Mytilopsis leucophaeata (Conrad, 1831)	6.093	0.796
Lasaeidae		
Mysella planulata (Stimpson, 1851)	0.492	0.137
Lucinidae		
Anodontia alba (Link, 1807)	0.062	0
Lucina pectinata (Gmelin, 1791)	0.203	0.011
Mactridae		
Mulinia lateralis (Say, 1822)	0.923	1.734
Rangia cuneata (Sowerby, 1831)	11.418	6.619
Spisula solidissima similis (Say, 1822)	0.031	0
Pharidae		
Ensis minor (Dall, 1900)	0.031	0
Pisidiidae		
Musculium partumeium (Say, 1822)	0.031	0.011
Pisidium sp.	0.008	0
Semelidae		
Abra aequalis (Say, 1822)	0.008	0
Solecurtidae		
Tagelus plebeius (Lightfoot, 1786)	5.604	4.553
Solenidae		
Solen viridis (Say, 1821)	0.016	0
Tellinidae		
Macoma constricta (Bruguiere, 1792)	0.515	2.662
Macoma tenta (Say, 1834)	0.102	0.056
Tellina versicolor (DeKay, 1843)	0.325	2.741
Tellina sp.	1.265	0.139
Veneridae		
Anomalocardia auberiana (d'Orbigny, 1842)	1.369	0.075
Chione cancellata (Linnaeus, 1767)	2.051	0.348
Cyclinella tenuis (Recluz, 1852)	0.161	0.059
Macrocallista nimbosa (Lightfoot, 1786)	0.016	0
Mercenaria campechiensis (Gmelin, 1791)	0.130	0
Veneridae (unidentified)	0.016	0
Arcoida		
Arcidae		
Anadara transversa (Say, 1822)	0.122	0.064
Noetiidae		
Noetia ponderosa (Say, 1822)	0.016	0
Mytiloida		
Mytilidae		
Amygdalum papyrium (Conrad, 1846)	0.261	4.268
Brachidontes modiolus (Linnaeus, 1767)	0	0.127
Geukensia granosissima (Sowerby, 1914)	1.201	2.793
Ischadium recurvum (Rafinesque, 1820)	1.861	1.780
Ostreoida		
Ostreidae		
Crassostrea virginica (Gmelin, 1791)	9.923	2.626
Dendostrea frons (Linnaeus, 1758)	0.445	0
Pectinidae		
Argopecten irradians (Lamark, 1819)	0.224	0
Anomiidae		
Anomia simplex (d'Orbigny, 1842)	0.916	0
Pterioida		
Pinnidae		
Atrina serrata (Sowerby, 1825)	0.010	0
Bivalvia (unidentified)	0.062	0.317
Mollusca (unidentified)	0.016	0.023
Total	94.929	81.765

Appendix 3. Dominance of all species as a percentage of all the mean number of individuals found in each site (river or creek) sampled.

	River or Creek										
Species	Alafia	Big Slough	Blackburn	Curry	Deer Prairie	Mud	Myakka	Peace	Shakett	Shell	Weeki
Corbicula fluminea	1.23	0	0	0	4.65	0	42.12	53.32	0	0.26	1.25
Polymesoda caroliniana	19.07	40	0	1.9	44.19	21.74	17.23	3.51	2.13	46.59	21.25
Rangia cuneata	0	24	100	0	51.16	0	8.86	5.79	0	30.9	0
Tagelus plebeius	3.69	28	0	34.18	0	30.43	9.54	1.36	24.63	19.31	23.75
Crassostrea virginica	21.88	0	0	5.7	0	26.09	0	1.06	27.59	0	25
Geukensia granosissima	29.44	0	0	0	0	0	6.22	0.22	0	0	0
Amygdalum papyrium	1.23	0	0	0	0	0	0	8.28	0	0	0
Neritina usnea	5.89	8	0	0	0	0	0.45	4.95	1.31	0.77	0
Ischadium recurvum	0	0	0	1.9	0	0	0.45	2.52	16.26	1.02	15
Littoraria irrorata	4.53	0	0	1.27	0	8.69	7.92	0.47	2.46	0.51	8.75
Macoma constricta	0	0	0	0	0	13.04	0	5.16	0	0	0
Chione cancellata	0	0	0	27.85	0	0	0	0	6.9	0	0
Tellina versicolor	0	0	0	0	0	0	0	5.42	0	0	0
Mulinia lateralis	1.71	0	0	3.8	0	0	2.49	2.44	0	0.13	0
Nassarius vibex	0	0	0	3.8	0	0	0.11	2.63	0.99	0	0
Mytilopsis leucophaeata	3.56	0	0	0	0	0	3.85	0	0	0.51	0
Haminoea succinea	0	0	0	0	0	0	0	2.1	0	0	0
Laevicardium mortoni	0	0	0	10.76	0	0	0	0	2.46	0	0
Tellina sp.	0	0	0	1.27	0	0	0	0	6.9	0	2.5
Bivalvia (unidentified)	4.35	0	0	0	0	0	0	0.1	0	0	0
Anomalocardia auberiana	0	0	0	1.27	0	0	0	0	3.94	0	0
Anadara transversa	0	0	0	3.8	0	0	0	0.06	0	0	0
Melongena corona	0	0	0	0	0	0	0	0.27	0	0	2.5
Mysella planulata	2.24	0	0	0	0	0	0	0	0	0	0
Cyclinella tenuis	0	0	0	1.27	0	0	0.11	0	1.97	0	0
Macoma tenta	0.66	0	0	0	0	0	0	0	0.99	0	0
Brachidontes modiolus	0	0	0	0	0	0	0	0.25	0	0	0
Lucina pectinata	0	0	0	1.27	0	0	0	0	0	0	0
Mollusca (unidentified)	0	0	0	0	0	0	0	0.01	0.99	0	0
Planorbidae (unidentified)	0.53	0	0	0	0	0	0	0	0	0	0
Polinices duplicatus	0	0	0	0	0	0	0.11	0.06	0	0	0
Cyrtopleura sp.	0	0	0	0	0	0	0	0	0.49	0	0
Musculium partumeium	0	0	0	0	0	0	0.08	0	0	0	0